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VARIATION VERSUS HEREDITY.[1]

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IN proposing to discuss this subject I have no new examples either of variation or heredity to describe, nor any new evidence to bring forward, with which to confirm established beliefs regarding these two well-known and important factors of biology. But I would like to call attention to a point of view from which variation, which we are accustomed to regard as a kind of accidental and abnormal performance of organisms, looms up into a prominence second to no other phenomenon of life, and stands out as the fundamental and distinctive characteristic of living beings. From this point of view, natural selection in all its different forms, the direct and indirect effects of environment, and other processes which, according to the orthodox view, are believed to be agencies in promoting evolution, appear but subsidiary steps in the acquirement of heredity, and are concerned only in checking evolution and in bringing the organism into a state of subjection to the mechanical laws of the physical environment in which they live.

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It is taken for granted that readers are familiar with the orthodox, or common working hypothesis, of modern naturalists in regard to these matters; but, in order that we may be thinking alike, let me mention a few particulars to which special attention is directed.

(*A*) It is assumed to be the accepted belief that *organisms acquire their distinctive characters by the processes of natural growth and development.*

(*B*) That it is the accepted belief that those characters which in a particular organism are *like* the characters of its parents and ancestors are to be explained on the hypothesis of *heredity, i.e., that organisms naturally reproduce offspring like themselves.*

(*C*) That it is the accepted belief that the characters which are *unlike* those of the parents are explained on the hypothesis of *variation, i.e., that organisms differ slightly or vary naturally from their immediate ancestors.*

It will be noticed that the term *organisms* in the second statement refers to the *parents* in the case; in the third statement it refers to the *developing offspring.* I understand this to be the accepted view, *i.e.*, that it is assumed that the *causative factor* determining the hereditary reproduction of *like* characters is associated with the *parent;* and, on the other hand, that the causative factor of *diversity* is associated with the *individual varying* in response to diversity in the conditions under which it develops. Or, to put this whole idea definitely as a separate proposition,

(*D*) It is the orthodox hypothesis, regarding this question, that *an organism arising under conditions entirely similar to those of its immediate ancestors, would not vary from them, but would develop in perfect facsimile to them;* and, therefore, that *variation is incident to heterogeneity of environment.*

Is all this true? Or is not the very converse of it true? In opening the discussion of this question, let me refer to the opinions of the founders of the evolution theory on this point.

In the year 1861 Darwin wrote to Thomas Davidson: "My greatest trouble is, not being able to weigh the direct effects

of the long-continued action of changed conditions of life, without any selection, with the action of selection or mere accidental (so to speak) variability. I oscillate much on this head, but generally return to my belief that the direct action can have played an extremely small part in producing all the numberless and beautiful adaptations in every living creature" (*Life and Letters*, vol. ii, p. 369).

Fifteen years later, in 1876, in a letter to Moritz Wagner, is found the following statement: "In my opinion the greatest error which I have committed has been not allowing sufficient weight to the direct action of environment, *i.e.*, food, climate, etc., independently of natural selection" (*Life and Letters*, vol. iii, p. 159); and in the following year, 1877, he wrote Malchior Neumayr: "There can now be no doubt that species may become modified through the direct action of the environment" (vol. iii, p. 232). The above quotations show where Darwin located the cause of variation, both when writing the *Origin* and in the later period of his life.

Again, in a letter to Lyell, in 1860, we find this statement: "Talking of 'Natural Selection,' if I had to commence *de novo*, I would have used 'natural preservation'" (vol. ii, p. 346). And, in 1863, to Asa Gray, Darwin wrote: "I have sometimes almost wished that Lyell had pronounced against me. When I say 'me' I only mean *change of species by descent.* That seems to me the turning point. Personally, of course, I care much about Natural Selection; but that seems to me utterly unimportant compared to the question of Creation or Modification" (vol. ii, p. 371).

These letters show where Darwin placed the emphasis in his life work. *Modification of species by descent* is the great discovery, and natural selection and direct effects of environment he believed to be the chief factors in bringing about this modification; but they were really secondary to the great fact of simple evolution, or the modification of organisms in the course of descent.

His letters leave no doubt that what he meant by "Natural Selection" was "Natural Preservation"; the "Survival," as Spencer put it, of characters which have already arisen in

ancestors by variation, and, after being tried by experience, are found favorable to the organism possessing them, and are, therefore, reproduced in their offspring. Cope and Henslow and others have called attention to this unmistakable meaning of natural selection. And Wallace, in 1866, criticised Darwin's use of the term "Natural Selection" by saying, "Nature . . . does not so much select special varieties as exterminate the most unfavorable ones."

On the other hand, the recognition of the view that variation is the prime factor of evolution, was evidently in the minds of both Lyell and Asa Gray, and was one of the chief causes of their hesitation, at first, to accept in full Darwin's theory of evolution. But, as a theory to explain the *origin of species*, Darwin was right, for the fundamental characteristic of species is not variation, but the *persistent reproduction of like characters*, and natural selection and the direct and indirect effects of environment are the most potent agencies discovered in determining this persistent uniformity of reproduction. But producing uniformity is not evolution.

The founders of the modern theory of evolution, while they were united as to the modification of species by descent, and in assuming that natural selection and kindred agencies were conspicuous factors in the general process of evolution, were not uniform in the assignment of the part played by these factors. Nevertheless, in the expressions of philosophical opinion regarding these points, above quoted, we find they were aware that the immediate effect of natural selection, etc., was in the direction of making characters hereditary, in "preserving" them in the reproductive sequence of the race. With the preconception, and as I believe misconception, that heredity is the essential characteristic of living organisms, it was necessary to believe that the organism could not, *of itself*, evolve into something different; hence the natural conclusion that variation must be *induced* by external agencies, and natural selection, etc., are these agencies which stimulate and promote variation, and at the same time check and hinder it. Herein lies one of the great inconsistencies of the orthodox theory.

The point of view suggested in this paper corrects some of these inconsistencies.

One of the difficulties, which seems to be removed by the new point of view, is seen by noting the simple phenomenon which takes place in any concrete case of natural selection.

First: In any particular case of selection it is necessary *that some character*, which has appeared for the first time in the course of the growth of a particular organism, *should reappear in its offspring*. The character is said to be "transmitted"; it "survives"; it is "preserved" in the offspring. In order to be thus "preserved," it ceases to be a divergent and variable element in individual growth, and becomes a regular or hereditary character in the descendants.

So far as the character itself is concerned it was produced without any precedent before it was found to be either profitable or unprofitable, and in being preserved it is simply reproduced. So far as the principle of modification is concerned, the offspring which reproduces the variable character of its parent is *less* variable than its parent, and if natural selection causes the preservation of the character, to that extent it is effective in checking evolution.

Secondly: It is to be observed *that that which takes place in the varying individual differs in degree, not in kind, from the ordinary processes of growth, or individual development.* Variation is not some peculiar mode of action of an organism, but it is the same process by which the individual builds up its hereditary characters. In the ordinary growth, as the organism develops from the germ to the adult each step of progress in development is, for the cells undergoing the development, a process of variation from the behavior of the parent cells from which they arose. So long as the varying does not exceed the varying of previous organisms, the process is called individual development, and is purely hereditary. Whenever the varying results in producing structure not hitherto produced, it is evolution.

On the assumption that this hereditary process of reproduction is a necessary and fundamental function of organisms, it is necessary to assume that some new law comes into opera-

tion where development ends, and variation, the first step in evolution, begins. Whereas, in fact, it is difficult even to imagine how the closest possible scrutiny of the growing individual could detect the place where normal development ends and variation begins.

Variation, in any concrete case, is simply the development of the individual in some different way, or to a degree beyond the attainment of its parents; but it is, nevertheless, normal constructive development. The whole secret of individual development lies in the fact that in the reproduction of growing cells, the daughter cells are slightly different from the parent cells, greater uniformity occurring in each mass of the same tissue or organ, but absolute uniformity nowhere. The multiplication of similar cells in growth, and their gradual modification in the construction of dissimilar tissues and organs in development, are phenomena no less diverse than is the hereditary process of reproduction of individuals from the variational production of specific differences. Variation is exhibited whenever an organic body produces another body dissimilar to itself, whether that body be a cell or an individual. Heredity is exhibited in both cases in the phenomenon of reproducing that which has already appeared.

Thirdly: Let us take another view of the subject and note *the relation which variation and heredity bear to experience.* In any concrete case of a growing organism the construction of a character according to heredity implies the experience of having previously constructed such a character, on the part of the parent, which is conceived of as the controlling cause of the process. Variation, on the other hand, is, when it first occurs, spontaneous, in so far as that means previous to experience. So far as the individual, or the race to which it belongs, is concerned, the varying act is an original act; it does not depend upon specific experience. Heredity is, therefore, of the nature of habit or memory, and implies experience. Variation is, in its intrinsic nature, original and genetic.

Selection is one of the steps in the acquirement of heredity, and thus the "origin of species" by natural selection is the acquiring of a regular, or hereditary, method of development

for each series, or race of organisms, breeding and developing together under like conditions.

If varying brings about modifications which are beneficial, then that which promotes varying must be an advantage. But in order to originate a species, varying is checked, and it is only as natural selection checks, transmits, and preserves, *less variably*, the characters acquired by variation that the origin of species results.

Thus we discover that the application of this hereditary principle to organisms, as a fundamental characteristic of living processes, makes it necessary to assume that evolution does not work in harmony with it; but only by checking, antagonizing, and violating heredity is any progress attained.

On the other hand, on the view that variation is the ultimate principle of all vital phenomena and is operative (as it is known to be) prior to experience, evolution becomes the fullest expression of life, and heredity and relative uniformity of reproduction the most natural expressions of the economical adjustment of living organisms to the limitations of environment. Evolution, in other words, takes place, naturally, as fast as the construction of organization and adjustment to environment furnish the possible medium for its expression. On this hypothesis evolution becomes as natural and universal a process for organic bodies as gravitation is for physical bodies.

Fourthly: According to the current philosophy of evolution, struggle for existence is assumed to be a most important factor in determining the course of "selection," or "preservation," by which advance is made. This struggle for existence is assumed to operate in the way of overcoming competitors for the same sources of good; and fitness to survive is measured by the capacity to grow big.

This theory, that measure of success is amount of food an organism can assimilate, that growing fat is evidence of fitness to survive, is consistent with the belief that repetition of the characters of ancestors, or heredity, is the primary law of organisms; and it is this philosophy which would lessen competition as a means of promoting progress.

But we have only to observe the natural course of the history of every organism to see that the setting up of antagonisms is not only the fundamental but the necessary law of organisms.

The most strenuous struggle which occurs in the life of any organism is that which separates it from its closest ancestor, its most intimate helper, the source, at the time of the separation, of all its good. No struggle with competitors, afterwards, equals in proportionate expenditure of energy this one. In the higher animals the term *labor* has been applied to it, because all other labor is but a faint imitation of it.

This greatest and universal struggle is the means of breaking with ancestry and setting up independence. So far as the immediate parent is concerned, the amount of energy expended in preparing for, caring for, and building up this offspring, which must necessarily increase and not diminish the total difficulties of living, is in excess of any other kind of energy put forth by the organism. And as to the offspring itself, the separation from the parent is a departure from almost total dependence and inactivity into increasing struggle and labor.

Thus in this process, which we are apt to associate most intimately with the law of heredity, is seen in operation this principle of doing otherwise, of departure from the bonds of heredity, of variation from the immediately preceding course of action of the individual performing the acts. It seems to us, as we ascend a mountain, as if the rough things in the path were the real hindrances to progress, but the fact is that the great work of a climber is always spent in overcoming the gravitation which would keep him at the bottom, and adjustment to the rocks on the way of his path is an insignificant part of his task. So it is not so much the local impediments of environment as the inertia of heredity which has to be overcome in each step of progress of evolution.

Malthus's theory rests on the assumption that there are more applicants than there are goods ; but whether this be true or not, it is certainly true that the greatest kind of human success we know of, and the most conspicuous examples of success, are those cases in which hitherto useless, because unused, sources of good are appropriated and their value realized, and thus the

way to new resources is opened. On the other hand, it is reliance upon ancestry, personal inactivity, failure to struggle, refusal to put forth the energy possessed, that constitute the curses of all organisms; and it is such evils that natural selection is constantly eliminating in the struggle for existence and the survival of the fittest. The first sign of headship and leadership and fitness to survive is a declaration of independence from the bonds of heredity. The place of greatest resistance, of hardest struggle, must be overcome before real progress can be made, and it is success there which is the first sign of fitness to survive and to perpetuate the race.

The very essence of virility, as of all evolution, consists in doing otherwise, — in varying from the past, in transgressing tradition, not violating but surpassing the laws of heredity. And the measure of success in such struggle is not accumulation of resources, but increase of productiveness. The most successful is the one which gets most result out of the resources at hand, and such success survives. But this is the law of variation, not heredity.

Fifthly: In order further to test the correctness of this hypothesis, it is important to examine the real *meaning of this phenomenon of variability.* What is the real fact to which attention is called by saying a species or an organism varies? Is there only a rearrangement of unchanging atoms? Is there something new originated? And what is the result of varying?

Darwin's theory of pangenesis, and the various other attempts, up to the most elaborate of all, Weismann's theory of germ plasm, which conceive of some sort of physical basis for the differences which arise in organic processes, are an indication of a belief that evolution does not originate anything new, that it merely seems to do so; and that organisms, like inorganic bodies, are substantially immutable. This mechanical theory provides for two categories, — things and acts, — into which objective phenomena may be distributed: things whose chief distinction is that they are posited and extended in space, and acts posited and extended in time. We cannot observe anything as absolutely inactive, nor can we observe any real act separated from some form of thing. But in imagination

the physicist abstracts the thing-in-itself, or the substance of things, as matter, which in its ultimate nature, as atoms, is unchangeable — immutable. In like manner, he abstracts from experience the substantial basis of observed actions and calls it energy. Thus in the working hypothesis of physics, the substantial basis of particular acts is energy, exactly as the substantial basis of particular things is matter. But the physicist finds no place in this hypothesis for any variation in the ultimate kind, amount, or constitution of these two substantial bases of experience. All differences in phenomena are, to this theory, different arrangements of immutable units.

The application of this hypothesis, of the immutability of the essence of things, to the phenomena of living organisms requires us to assume that there are some kinds of ultimate immutable units back of organisms, which necessarily behave uniformly, except as they may be diverted by the action of some force from outside. Thus, I suppose, has arisen the almost universal belief that the uniform behavior of organic bodies, which we define by the term *heredity*, is a necessary and fundamental characteristic of organic units, just as inertia is a characteristic of inorganic bodies. The final outcome of this view is the assumption of the existence of separate and immutable units for every divergent phenomenon of organisms. Darwin evidently adopted some such view, and I do not see that the followers of Darwin have escaped this fundamental conception in elaborating the general evolution hypothesis. But the first step toward correcting it was taken when the idea of immutability was dissociated from the organic species.

Cuvier was the last of the great naturalists to maintain the immutability of species. It was the recognition of the intrinsic mutability of the organic species that made a rational theory of evolution possible, and it is my sincere conviction that a consistent theory of evolution cannot be built up which stops here. I cannot discover that there is any halting place. In order to explain the wonderful phenomena of organisms, the principle of mutability must be extended to the ultimate units of which every living body is composed. Not only the species, but the individual, the cell, the units which constitute the living

form of protoplasmic matter, must be conceived of as in a normal state of mutability.

That which makes an organic body to be vital, and distinguishes it from matter in an inorganic state, is this constant and incessant varying.

Recognizing this as the fundamental characteristic of living matter, it is very easy to conceive how varying will proceed constantly and in all directions, like a gas expanding, except when checked and guided by the impact and restraints of external conditions.

I have now stated briefly the meaning of the proposition that *variation, and not heredity, is the fundamental characteristic of the phenomena of organisms*, and a few of the arguments which recommend this view to consideration and acceptance as a working hypothesis for future investigation.

These arguments may be stated briefly as follows :

First : In any concrete case of natural selection, or similar processes, the actual result of selection is the retarding and checking of variation ; and the offspring necessarily evolves more slowly than its parent, in direct proportion to the efficacy of the natural selection.

Secondly: That the organic processes by which variation takes place in an organism differ from the ordinary process of development in individual growth only by passing beyond the limit reached by the ancestor; and hence variation is but a phase of the fundamental genetic process peculiar to living organisms.

Thirdly: That every act of variation is anterior to experience, and thus is necessarily original and genetic, whereas every hereditary act is necessarily secondary to, and the result of, experience, and that the law of heredity must, therefore, be acquired in the process of evolution, and is not fundamental.

Fourthly: That, as to struggle for existence, the most strenuous effort that is made (both by the parent and by the offspring) in the course of organic processes is that which produces antagonism of interests. On the part of the parent, it parts with that which has cost it the greatest expenditure of energy ; and on the part of the offspring, the result is the loss, in part or wholly, of the only source of its living up to the moment of the struggle.

Fifthly: That the orthodox view of the case is inconsistent, in so far as it recognizes mutability as applicable only to organic species, and clings to the idea of immutability of the more fundamental units of biology, *viz.*, the individual, the cell, and the protoplasmic states of matter.

These considerations bring us to a point of view in which heredity and variation hold a different relation to evolution than in the ordinary working hypothesis of biology.

If this point of view presents the facts in their true relations, we must seek for the immediate determining causes of variation, not in natural selection, nor in any of the environmental conditions, either direct or indirect, by which hereditary repetition is established, but in the phenomena of individual growth and development, and in the more fundamental processes of cell growth and metabolism.

NEW HAVEN, CONN.,
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